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Species richness of polydorid species (Polychaeta: Spionidae) in the English Channel (France) and on the Pacific Coast of Tohoku District (Japan)

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Abstract: Successive polychaete inventories have reported polydorids in the English Channel and there are some reports describing polydorids from the Pacific coast of Tohoku District, Japan. Species Richness in both areas is compared and discussed. Moreover, in March 2018, French-Japanese collaboration led to the collection of polydorid species from the shells of feral and cultured oysters *Crassostrea gigas* (THUNBERG, 1793) along the western coast of Normandy, France. Some species were also extracted from coralline algae and other calcareous substrates. Eight species were recorded belonging to four genera: *Boccardia, Boccardiella, Dipolydora* and *Polydora*. The two species *Polydora hoplura* Claparède, 1868 and *Dipolydora giardi* (Mesnii, 1893) were previously known in Normandy, along with another member of the genus *Dipolydora* that has not been identified to the species level. *Boccardia proboscidea* Hartman, 1940, *Boccardiella hamata* (Webster, 1879) and *Polydora websteri* Hartman in Loosanoff & Engle, 1943 represent new records in Normandy, while both *Boccardia pseudonatrix* Day, 1961 and *Polydora onagawaensis* Teramoto, Sato-Okoshi, Abe, Nishitani, Endo, 2013 are new species for European waters. We point out that collaboration with polychaete specialists to study well-known seas such as the English Channel would allow us to discover new species, expanding the list of species actually present. This study also highlights the need to continue this partnership further identify which polychaete species infest English Channel oysters.

Keywords : *polydorids, English Channel, new recorded species, Tohoku District*

1. Introduction

The polydorids (Annelida: Spionidae) contain nine genera: i.e. *Amphipolydora* Blake, 1983, *Boccardia* Carazzi, 1893, *Boccardiella* Blake & Kudenov, 1978, *Carazziella* Blake & Kudenov, 1978, *Dipolydora* Verrill, 1881, *Polydora* Bosc,

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1802, *Polydorella* Augener, 1914, *Pseudopolydora* Czerniavsky, 1881 and *Tripolydora* Woodwick, 1964, with each of them having a modified fifth chaetiger. Identification of polydorids remains problematic due to numerous confusions of species and their unknown distribution: i.e. several introduced species occur around the world ocean (Simon and Sato-Okoshi, 2015). Moreover, many polydorid species are known as borers in calcareous substrates, and have been reported to inhabit various types of living and non-living calcareous structures including mollusc shells, corals and coralline algae (Sato-Okoshi, 1999; Sato-Okoshi *et al*., 2015, 2017; Abe *et al*., 2019). These borers cause severe damage to their calcareous hosts, and polydorid infestation is considered as a serious problem in aquaculture especially for oysters (Ruellet, 2004; Simon and Sato-Okoshi, 2015). *Crassostrea gigas* (Thunberg, 1793) was introduced from Japan and, during the 1970s, was cultivated in large quantities along the French coast (Koike, 2015). Ruellet (2004) was the first to investigate in detail the polydorid infestation of *C. gigas* in Normandy, showing that cultured oysters were more affected on the eastern coast of the Cotentin peninsula. He identified four species, *Boccardia polybranchia* (Haswell, 1885), *Boccardia semibranchiata* Guérin, 1970, *Polydora ciliata* (Johnston, 1838) and *Polydora hoplura* Claparède, 1868, as well as a species of the genus *Boccardia*, which regularly colonize oysters cultivated in Normandy. Duault *et al.* (2001) in their study of the infestation of polydorids on *C. gigas* along the French Atlantic coast in 1999 had accounted until 100 worms per oyster in Normandy where the infestation reaches its maximum in the western part of the Bay of Seine. In addition, the coast of the department of Calvados is partly characterized by a limestone rocky platform strongly infested by polydorids with up to 300,000 individuals per m^2 (Ruellet, 2004). Moreover, north-west residual currents favour the transport of polydorid larvae towards the east coast of the Cotentin, where shellfish farms are located (Salomon and Breton, 1981). This continuous water flux and enhanced supply of larvae probably explains the high infestation level observed in oysters on the eastern Cotentin coast from Quineville to Saint-Vaast-La-Hougue. Polydorids create mud blisters that hinder the marketing of oyster products in contaminated areas of the eastern basin of the east Cotentin (Ruellet, 2004; Royer *et al*., 2006).

Royer *et al.* (2006) examined the presence of polydorids and other epibionts found on the Pacific oyster *C. gigas* from the Bay of Veys on the western part of the Calvados coast. Although no significant effect of polydorid infestation could be observed to explain the summer mortality of oysters, it has been demonstrated that polydorids have a significant negative effect on host growth. Abundant mud blisters on the inner shell layer are associated with reduced meat and shell weight, thereby causing a potential decrease in oyster productivity. Ruellet (2004) and Royer *et al.* (2006) carried out a detailed study of the impact of massive infestation by *Polydora* on oyster life traits, but they did not identify the species colonizing the oysters. While the study of the infestation of polydorids in Normandy is of biological and aquacultural importance (Duault *et al*., 2001; Ruellet, 2004; Royer *et al*., 2006), the identification of species and their centres of origin nevertheless remains unclear.

In the 1960s, oyster farming in France was greatly affected by the mass mortality of the Portuguese oyster *Crassostrea angulata* (Lamarck, 1819), caused by a viral disease and infection from the parasitic protozoans *Marteilia* and *Bonamia* (Grizel and Heral, 1991; Okoshi

and SATO-OKOSHI, 1996). To restore the oyster industry after this catastrophic event, the first mass exportation of spat of the Pacific oyster *C. gigas* occurred from Japan (Sanriku coast on the Pacific shore of Tohoku District, especially from Sendai Bay) to France. This trial took place successfully in 1969 and the project was continued until 1979 (KOGANEZAWA, 1984; KOIKE, 2015). Therefore, to summarize the recent studies on polydorid species infesting oyster shells from the English Channel and Japanese waters it is worthwhile to consider the problem of the introduction of non-native species.

In this review, we summarize the previous studies of polydorids in two sea areas: the Atlantic coast of France, especially the English Channel, and along the Pacific coast of northeastern Japan. In both areas oyster farming is popular and large numbers of oysters have been produced and exported/imported over the past 100 years, which offers perspectives for the development of future joint research between France and Japan.

2. English Channel

2.1 Previous Inventory

The English Channel is a shallow epicontinental sea with a maximum depth of 174 m bordering the coasts of the United Kingdom to the north and France to the south. The shoreline is characterized by a wide variety of landforms, with retreating rocky coasts, sand/gravel beaches, rias and estuaries, as well as sandy beach/dune strand-plains and extensive intertidal flats and marshes (DAUVIN, 2019). The French coast of the western Basin is characterized by rocks that form eroding cliffs, associated with small, sandy pocket beaches, and relatively small rias and estuaries. On the shores of the eastern Basin, along the coast of the Pays de Caux, high chalk cliffs are associated with narrow beaches of sand and gravel (flint/chalk). The English Channel is one of the most anthropogenically affected marine areas in the world. It has attracted numerous industrial activities such as maritime transport, dredging and sediment dumping, granulate extraction, tourism, fisheries, aquaculture and offshore wind-farm projects (DAUVIN, 2019). The French side of the Channel is an important area for aquaculture, principally the Pacific oyster *C. gigas* and the mussel *Mytilus edulis* Linnaeus, 1758. With a current annual production of $>$ 16,000 t of oysters and 35,000 t of mussels, supporting around 500 jobs in the aquaculture industry, the Normandy region is among the leaders of bivalve aquaculture in Europe (DAUVIN, 2019).

There is a long history of invertebrate inventories compiled mainly by marine biological stations such as Roscoff and Dinard in Brittany, Plymouth in England, Luc-sur-Mer in Normandy and Wimereux along the Opal coast in the eastern part of the English Channel. As a result, a total of 13 polydorid species have been reported in the English Channel (FAUVEL, 1927; DAUVIN *et al*., 2003; RUELLET, 2004, LE MAO *et al*., 2020) (Table 1). FAUVEL (1927) reported the presence of 10 species including three shell-boring parasites of the oyster *Ostrea edulis* Linnaeus, 1758: *Dipolydora coeca* (Örsted, 1843) (referred to as *Polydora*), *Dipolydora flava* (Claparède, 1870) (referred to as *Polydora*) and *P. hoplura*, while RUELLET (2004) reported five shell-boring parasite species of the oyster *C. gigas* in Normandy, on both the western and eastern coasts of Cotentin: *Boccardia polybranchia*, *B. semibranchiata,* an unidentified *Boccardia, Polydora hoplura* and *P. ciliata*. FAUVEL (1927) is the only author to have examined the polydorids and their distribution before the introduction of Pacific oysters in Normandy.

Table 1. Polydorid species reported along the French coast of the English Channel in the successive inventories. *Presence not confirmed in the English Channel.

Species Worms 2021	Fauvel, 1927	Dauvin *et al*., 2003	Ruellet, 2004	Le Mao *et al*., 2020	Sato-Okoshi *et al*., 2022
Polydora ciliata (Johnston, 1838)	*Polydora ciliata* (Johnston)	*Polydora ciliata* (Johnston, 1838)	*Polydora ciliata* (Johnston, 1838)	*Polydora ciliata* (Johnston, 1838)	
Polydora hoplura Claparède, 1868	*Polydora hoplura* Claparède	*Polydora hoplura* Claparède, 1870	*Polydora hoplura* Claparède, 1870	*Polydora hoplura* Claparède, 1869	*Polydora hoplura* Claparède, 1868
Dipolydora giardi (Mesnil, 1893)	*Polydora giardi* Mesnil	*Polydora giardi* Mesnil, 1896	*Dipolydora giardi* (Mesnil, 1893)	*Dipolydora giardi* (Mesnil, 1896)	*Dipolydora giardi* (Mesnil, 1893)
Dipolydora coeca (Örsted, 1843)	*Polydora caeca* (Œrted)	*Dipolydora coeca* (Oersted, 1843)	*Dipolydora coeca* (Oersted, 1843)	*Dipolydora coeca* (Örsted, 1843)	
Dipolydora flava (de Claparède, 1870)	*Polydora flava* Claparède	*Polydora flava* Claparède, 1870	*Dipolydora flava* (de Claparède, 1870)	*Dipolydora flava* (Claparède, 1870)	
Dipolydora quadriloda (Jacobi, 1883)	*Polydora quadrilobata* Jacobi	*Polydora quadrilobata* Jacobi, 1883*		*Dipolydora quadrilobata* (Jacobi, 1883)	
Dipolydora caulleryi (Mesnil, 1897)	*Polydora Caulleryi* Mesnil	*Polydora caulleyri* Mesnil, 1897	*Dipolydora caulleryi* (Mesnil, 1897)	*Dipolydora caulleryi* (Mesnil, 1897)	
Dipolydora armata (Langerhans, 1880)	*Polydora armata* Langerhans	*Polydora armata* Langerhans, 1880	*Dipolydora armata* (Langerhans, 1880)	*Dipolydora armata* (Langerhans, 1880)	
Boccardia polybranchia (Haswell, 1885)	*Polydora* (*Boccardia*) *polybranchia* Haswell	*Boccardia* (*Polydora*) *polybranchia* Hasxell, 1885	*Boccardia polybranchia* Hasxell, 1885	*Boccardia polybranchia* (Haswell, 1885)	
Pseudopolydora antennata (Claparède, 1868)	*Polydora* (*Carazzia*) *antennata* Claparède	*Pseudopolydora antennata* Claparède, 1870	*Pseudopolydora antennata* Claparède, 1870	*Pseudopolydora antennata* (Claparède, 1869)	
Pseudopolydora pulchra (Carazzi, 1893)		*Pseudopolydora pulchra* Carazzi, 1895	*Pseudopolydora pulchra* (Carazzi, 1893)	*Pseudopolydora pulchra* (Carazzi, 1893)	
Boccardiella ligerica (Ferronnière, 1898)		*Boccardia ligerica* Ferronnière, 1898.	*Boccardiella ligerica* (Ferronnière, 1898)		
Boccardia semibranchiata Guérin, 1970			*Boccardia semibranchiata* Guérin, 1970		
Boccardia proboscidea Hartman, 1940					*Boccardia proboscidea* Hartman, 1940
Boccardia pseudonatrix Day, 1961					*Boccardia pseudonatrix* Day, 1961
Boccardiella hamata (Webster, 1879)					*Boccardiella hamata* (Webster, 1879)
Polydora onagawaensis Teramoto, Sato-Okoshi, Abe, Nishitani & Endo, 2013					*Polydora onagawaensis* Teramoto, Sato-Okoshi, Abe, Nishitani, Endo, 2013
Polydora websteri Hartman in Loosanoff & Engle, 1943					*Polydora websteri* Hartman in Loosanoff & Engle, 1943
					Dipolydora sp

2.2 Recent prospection

New sampling of polydorids took place in March 2018 at six sites around the Cotentin peninsula and on the western part of the Calvados coast, from *C. gigas* oyster farms as well as from feral oysters, limestone substrates and calcareous algae (Fig. 1) (see Sato-Okoshi *et al*., 2022 for details). A total of eight species were identified using morphology and gene sequences (Table 1) (Sato-Okoshi *et al*., 2022): two *Boccardia* species were found (*B. proboscidea* and *B. pseudonatrix* Day, 1961) as well as

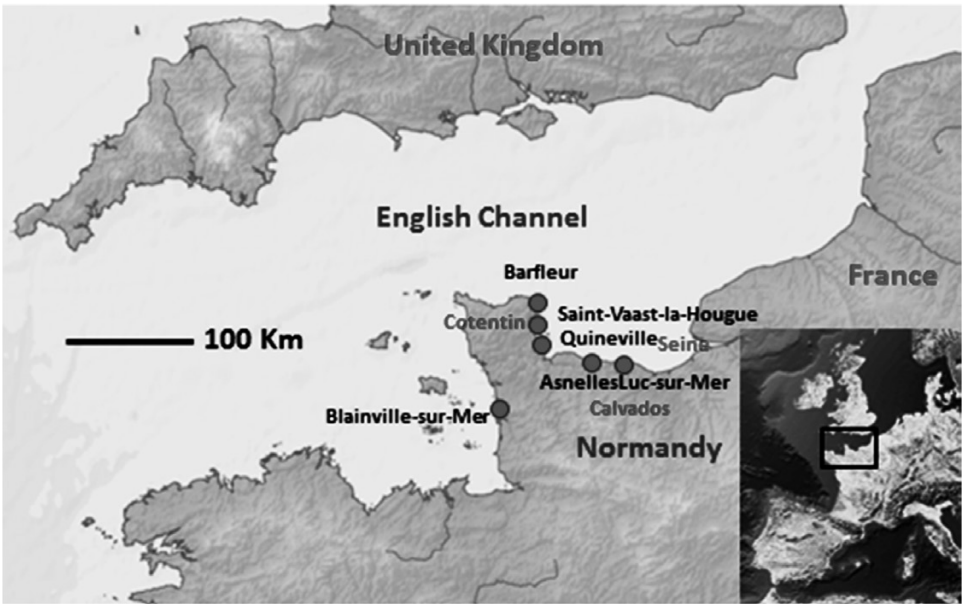

Fig. 1 Location of the sites (closed circles) visited in Normandy in March 2018.

Boccardiella hamata (Webster, 1879), two *Dipolydora* (*D. giardi* (Mesnil, 1893) and one unidentified *Dipolydora*) and three *Polydora* (*P. hoplura*, *P. onagawaensis* and *P. websteri*).

2.2.1 Species previously known in Normandy and in the English Channel

Dipolydora giardi

This species has been reported at Blainville-sur-Mer in the cultured oyster *C. gigas*. It is widely distributed from the western part of the English Channel to the Bay of Seine (Dauvin *et al*., 2003; Ruellet, 2004). Found at low tide in *Lithothamnium* calcareous algae, in the crampons of kelp forests (Fauvel, 1927) and as a shell-boring parasite in the Normandy oyster (Ruellet, 2004).

Polydora hoplura

This species is reported at Blainville-sur-Mer in feral and cultured *C. gigas* oysters. *P. hoplura* is widely distributed from the western part of the English Channel to the Bay of Seine (Dauvin *et al*., 2003; Le Mao *et al*., 2020). It is found in the intertidal zone and shallow waters, among Serpulid polychaetes and in the oyster *O. edulis* as a shell-boring parasite (Fauvel, 1927).

2.2.2 Species recently reported for the first time in the English Channel

Boccardia proboscidea

Sato-Okoshi *et al.* (2022) reported the first record in Normandy from the Cape of Barfleur on coralline algae and in cultured *C. gigas* from Asnelles investigated in 2018. Pezy *et al.* (2021) listed this species as probably occurring in Normandy. Our record confirms this proposition.

Boccardia proboscidea was originally described from the west coast of the United States (California) and has been recorded along the French coast of the English Channel, on the Opal coast in the north of France in 2014 (Spilmont *et al*., 2018), in north Brittany in 2018 (Gully and Cochu, 2020), and in the southern part of the

North Sea both along the Belgian and Dutch coasts (KERCKHOF and FAASSE, 2014). It has also been reported from North-west Scotland waters in the UK (HATTON and PEARCE, 2013) and in the south of the Bay of Biscay along the Basque coast (JAUBET *et al.*, 2010), as well as along the French Atlantic coast near La Rochelle (SPILMONT *et al.*, 2018). It has been widely observed on the coasts of the Pacific Ocean: Canada (SATO-OKOSHI and OKOSHI, 1997), United States, Japan (SATO-OKOSHI, 2000, ABE *et al.*, 2019), Australia, South Africa, Argentina (see GULLY and COCHU, 2020 for references therein). In most places, it is considered as an introduced and invasive species (JAUBET *et al.*, 2010, 2014, 2018). Its populations are well established in European waters.

Boccardiella hamata

SATO-OKOSHI *et al.* (2022) reported the first record of this species in the English Channel in feral *C. gigas* at Saint-Vaast-la-Hougue. PEZY *et al.* (2021) listed this species as probably occurring in Normandy. Our record confirms this proposition. This species was originally described from the Atlantic coast of North America, and it is now commonly known from the Pacific coasts, e.g., Vancouver Island, Canada (SATO-OKOSHI and OKOSHI, 1997), Japan (SATO-OKOSHI, 2000, ABE *et al.*, 2019), China (ZHOU *et al.*, 2010), Korea (SATO-OKOSHI *et al.*, 2012). It was recently reported in the southern North Sea from Belgium and the southwestern Dutch delta (KERCKHOF and FAASSE, 2014). The species lives in muddy environments as well as amongst Pacific oysters on artificial hard substrates such as coastal defence structures (KERCKHOF and FAASSE, 2014). It has recently been found inhabiting sponges (ABE *et al.*, 2019).

Polydora websteri Hartman in Loosanoff & Engle, 1943

SATO-OKOSHI *et al.* (2022) reported the first record of this species in Normandy on the eastern coast of the Cotentin peninsula at Quineville, and from Asnelles, on cultured oyster *C. gigas* investigated in 2018. Studies carried out in 2017 show that *P. websteri* does not live in the shells of cultured oysters from Arcachon (SATO-OKOSHI *et al.*, unpublished data). It has also been reported recently in naturalized oyster reefs in the Wadden Sea (WASER *et al.*, 2020). *Polydora websteri* originates from the eastern coast of North America and is today recorded from many countries worldwide (SIMON and SATO-OKOSHI, 2015).

2.2.3 Species reported for the first time in European waters

Boccardia pseudonatrix Day, 1961

SATO-OKOSHI *et al.* (2022) reported this species for the first time in European waters from the eastern coast of the Cotentin peninsula, at Saint-Vaast-la-Hougue, on cultured *C. gigas* and at Quineville on feral *C. gigas* investigated in 2018. *Boccardia pseudonatrix* was originally described from South Africa, and was then reported from Australia and Japan (SATO-OKOSHI *et al.*, 2008; ABE *et al.*, 2019). The main characteristics are transparent palps with irregular colourless spots crossing transversely, giving the appearance as being crossed by white bars in lateral view; conspicuous black pigmentation on the prostomium and a mid-dorsal ridge from chaetiger 5 to the middle of chaetiger 8.

Polydora onagawaensis Teramoto, Sato-Okoshi, Abe, Nishitani & Endo, 2013

This species was found in the Bay of the Seine at Saint-Vaast la Hougue, on feral *C. gigas*, and at Quineville and Asnelles on the cultured *C. gigas*; it was also sampled from limestone and

calcareous substrates as well as on concrete blocks at Luc-sur-Mer investigated in 2018. The individuals of *P. onagawaensis* observed in Normandy show some morphological characteristics that are different compared with the Japanese *P. onagawaensis* (Sato-Okoshi *et al*., 2022). The specimens from Normandy can be morphologically distinguished from those collected in Japan (Teramoto *et al*., 2013) by the wider peristomium, occasionally strong intense black pigmentation around the base of both palps, maximum caruncle elongation up to the middle of chaetiger 3, and a smaller number of branchial chaetigers.

3. Pacific coast of Tohoku District

The Pacific coast of Tohoku District, located in north-eastern Japan, is characterized by a series of rias and a complex coastline that includes rocky reefs, sandy beaches, bays, and estuaries (Fig. 2). The bottom sediment varies from rock, gravel, sand to mud. The coastline faces the open sea. The Oyashio cold current and the Kuroshio warm current flowing along the coast make this area a rich fishing ground. As a result, the fishery industry is thriving in the coastal areas, with mollusc aquaculture such as oyster *C. gigas* (Okoshi *et al*., 1987) and scallops *Patinopecten* (*Mizuhopecten*) *yessoensis* (Jay, 1857). Sea squirts *Halocynthia roretzi* (Drasche, 1884), wakame seaweed *Undaria pinnatifida* (Harvey) Suringar, 1873 and nori seaweed *Neopyropia yezoensis* f. *narawaensis* (Kikuchi, Niwa & Nakada) Kikuchi & Niwa, 2020 are cultured subtidally, while salmon fish *Oncorhynchus kisutch* (Walbaum, 1792) introduced from the USA is cultured in the bays. The Tohoku coast has the following characteristic features: 1) located at a latitude of 40°N comparable to 50°N for the English Channel, 2) the area is relatively well researched, 3) a relatively similar length of coastline compared to the English Channel, and 4) there is a history of oysters being exported from the Pacific coast of Tohoku District to France.

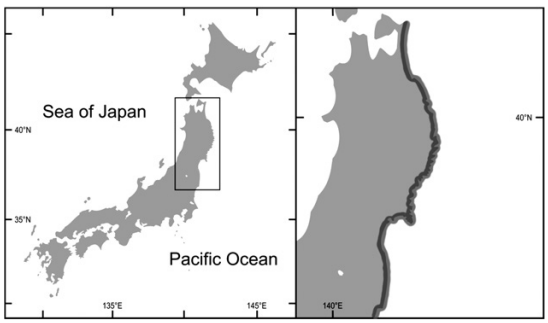

Fig. 2 Map of the Pacific Coast of Tohoku District, Japan. Fat line showing the Sanriku to Joban coast along the east coast of Tohoku District.

A total of nine shell-boring polydorid species have been reported from the southern part of the Pacific coast of Tohoku District, Japan (Sato-Okoshi, 1999; Sato-Okoshi and Abe, 2012, 2013), namely: *Dipolydora bidentata* (Zachs, 1933); *Dipolydora concharum* (Verrill, 1880); *Dipolydora giardi*; *Polydora brevipalpa* Zachs, 1933; *Polydora curiosa* Radashevsky, 1994; *Polydora hoplura*; *Polydora neocaeca* Williams & Radashevsky, 1999; *Polydora onagawaensis* and *Polydora websteri*.

In addition, ten other interstitial, epifaunal and infaunal polydorid species have been reported (Sato-Okoshi, 2000; Abe *et al*., 2016; Abe and Sato-Okoshi, 2021). These species are: *Boccardia proboscidea* (interstitial); *Boccardia pseudonatrix* (interstitial); *Boccardiella hamata* (Interstitial); *Dipolydora cardalia* (Berkeley, 1927) (infaunal); *Dipolydora socialis* (Schmarda, 1861) (interstitial, infaunal); *Polydora cornuta* Bosc, 1802 (infaunal, epifaunal); *Pseudopolydora achaeta* Radashevsky & Hsieh, 2000 (infaunal); *Pseudopolydora* cf. *kempi* (Southern, 1921) (infaunal); *Pseudopolydora paucibranchiata* (Okuda,

1937) (infaunal) and *Pseudopolydora* cf. *reticulata* Radashevsky & Hsieh, 2000 (infaunal). *Polydora neocaeca* and *B. pseudonatrix* have not yet been reported from the Pacific coast of Tohoku District, but they have been identified by the present authors (personal communication) from Sasuhama, Ishinomaki City and Moune Bay, Kesennuma City, respectively, in Miyagi Prefecture, north-eastern Japan.

4. Discussion

The species richness of polydorids from the Japanese Pacific coast of Tohoku District and the English Channel appears to be comparable, with 19 species and 18 species, respectively. Our 2018 surveys lead to the addition of two shell-boring species, *Polydora onagawaensis* and *P. websteri* and three non-boring species *Boccardia proboscidea, B. pseudonatrix* and *Boccardiella hamata*, to the list of the species present in Normandy and in the English Channel (Table 1) (Sato-Okoshi *et al.*, 2022). Moreover, the five newly added species are all oyster-associated species (shell-boring species or species inhabiting mud tubes in the crevices of the shell), and may have been transferred to these waters very recently.

All five genera (*Boccardia, Boccardiella, Dipolydora, Polydora* and *Pseudopolydora*) have been recorded in both Japanese waters and the English Channel.

Four boring species are common in both areas: *Dipolydora giardi, Polydora hoplura, P. onagawaensis* and *P. websteri*, as well as three non-boring species: *B. proboscidea, B. pseudonatrix* and *Boccardiella hamata*.

In his PhD thesis on oyster infestation of the Normandy oyster, Ruellet (2004) reported five species: *B. polybranchia*, *B. semibranchiata*, *P. ciliata* and *P. hoplura*, and an unidentified species of the genus *Boccardia*. Our 2018 survey (Sato-Okoshi *et al.*, 2022) was probably insufficient to establish the occurrence of all polydorids actually present in the shells of *C. gigas*. Nevertheless, *P. hoplura* is the only species cited by Ruellet that is in common between Normandy and Japan. Moreover, the unidentified *Boccardia* recorded by Ruellet may possibly correspond to one of the two species *B. proboscidea* and *B. pseudonatrix* identified during our survey in March 2018.

Boccardia semibranchiata was recorded by Ruellet (2004) only in the Bay of Veys. *Boccardia polybranchia* was reported in the Normano-Breton Gulf (Fauvel, 1927; Dauvin *et al.*, 2003; Le Mao *et al.*, 2020), in the Bay of Veys in the western part of the Bay of Seine (Ruellet, 2004). These two species were considered as Non-Indigenous Species (NIS) in Normandy by Pezy *et al.* (2021).

Even though Ruellet (2004) reported the presence of *Polydora ciliata* as a shell-boring parasite of *C. gigas* in Normandy, no *P. ciliata* was identified during our 2018 survey. However, this species was considered to be a non-boring species by Radashevsky and Pankova (2006) and our prospections concern mainly the oyster-boring species and species associated with oysters. Supplementary samplings are needed to verify the presence of *P. ciliata* in the English Channel, especially on rocky shores of the eastern basin along the Opal coast where the species was reported in very high abundances by Lagadeuc and Brylinski (1987).

5. Future perspectives

A total of 152 Non-Indigenous Species (NIS) introduced through human actions have been recorded in Normandy (Pezy *et al.*, 2021), with 54 NIS along the UK and French coasts of the English Channel originating from Japanese waters (Dauvin *et al.*, 2019). These 54 species

include 22 algae (7 micro-algae and 15 macro-algae) and 32 invertebrates: one Protozoan, two Hydrozoans, two Anthozoans, one Nematode, two Platyhelminthes, two Polychaetes (*Clymenella torquata* (Leidy, 1855) and *Hydroides ezoensis* Okuda, 1934), eight Crustaceans, one Insect, five Bryozoans, five Molluscs and four Ascidians. SATO-OKOSHI *et al.* (2022) show that *P. onagawaensis* described from Japanese waters is also present in the English Channel; however, its COI gene sequences are more similar to those of US specimens than to Japanese ones.

In the future, we need to determine the biogeographic origin of certain species, not only *P. onagawaensis*, but also *Boccardiella hamata*, *Boccardia proboscidea*, *B. peudonatrix* and *P. websteri*.

The dispersal of these polydorids can be attributed in large part through aquaculture of *C. gigas* with the introduction of oysters for commercial activities in new areas and the repeated transport of oysters back and forth between different areas. Since the actual distribution of many polydorid species remains unknown, supplementary studies should be undertaken to identify shell-boring species present along the French coast of the Mediterranean Sea (Thau basin) and Atlantic coast (Arcachon basin and Marennes-Oléron area) as well as in the English Channel (Normandy and eastern English Channel). Two main aspects should be studied: the presence and occurrence of shell-boring polydorid species in cultivated and feral *C. gigas*, as well as their centres of origin. However, it is clear that morphological observations alone will not be sufficient to achieve this aim and molecular tools are needed to resolve such issues. Since many species are already widespread, these molecular tools should be applied to specimens collected from several possible centres of origin. A real challenge for future collaborative research between Japan and France begins.

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